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Soil carbon stocks in tropical forests regulated by base cation effects on fine roots

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Tropical forests are the most carbon (C)-rich ecosystems on Earth, containing 25-40% of global terrestrial C stocks (1, 2). While large-scale quantification of aboveground biomass in tropical forests has improved recently (3), soil C dynamics remain one of the largest sources of uncertainty in Earth system models (4), inhibiting our ability to predict future climate (5). Globally, soil texture and climate predict < 30% of the variation in soil C stocks (1), so ecosystem models often predict soil C stocks using measures of aboveground plant growth (4). However, this approach underestimates tropical soil C stocks, and is inaccurate compared with estimates for data-rich northern ecosystems (6). By quantifying soil organic C stocks to 1 m depth for 48 humid tropical forest plots across gradients of rainfall and soil fertility in Panama, we show that soil C across these diverse tropical forests does not correlate with common predictors used in models, such as plant biomass or litter production. Instead, a structural equation model including base cations, soil clay content, and rainfall as exogenous factors and root biomass as an endogenous factor predicted nearly 50% of the variation in tropical soil C stocks, indicating a strong indirect effect of base cation availability on tropical soil C. The importance of cations shown here expands on long-standing work showing that phosphorus (P) commonly controls aboveground plant growth in tropical forests (7, 8). Including soil cations in C cycle models, and thus emphasizing mechanistic links among nutrients, root biomass, and soil C stocks, will improve prediction of climate-soil feedbacks in tropical forests.

Significance Statement

Tropical forest soils contain some of the largest stocks of carbon on Earth, making them of broad importance in the global carbon cycle. Nonetheless, our understanding of what drives

1 variation in soil carbon stocks across tropical landscapes is limited, inhibiting our ability to
2 predict large-scale responses to global change. This study revealed a strong effect of soil base
3 cations on soil C stocks via changes in root biomass. In contrast, aboveground plant growth was
4 not related to soil C stocks, contrary to ecosystem model assumptions. The 48 Panamanian
5 forests included here covered a two-fold range in rainfall, five soil orders, 25 geological
6 formations, and a 20-fold range nutrient availability, likely making our results applicable to a
7 much broader geographic range.

1 **Introduction**

2 Tropical forest soils contain some of the largest stocks of carbon on Earth, making them
3 of broad importance in the global carbon (C) cycle (1, 2). Aboveground C stocks and litterfall in
4 closed-canopy tropical forests can be measured with precision at large scales using remote
5 sensing (3), so extrapolating soil C stocks from aboveground measures with few *in situ* soil data
6 has formed the basis for many modeling efforts (4). However, aboveground plant metrics can be
7 poor predictors of soil C stocks globally, although there are few examples for lowland tropical
8 forests (6). While major increases in plant litterfall have been shown to influence C stocks at the
9 soil surface in tropical forests (9), most long-term C storage within mineral soils probably
10 originates from root biomass (10). Particularly in humid tropical forests, decomposition of leaf
11 litter on the forest floor is rapid (<3 years) (11), and a large proportion of surface litter is likely
12 respired back to the atmosphere as CO₂ rather than transported downward and stored in mineral
13 soils. Root C, in contrast, is transferred directly into mineral soils, where tough, lignin-rich
14 tissues, saturated conditions, and low oxygen levels can slow decomposition, leading to greater C
15 retention of root tissues relative to leaf litter (12, 13). Thus, estimates of root biomass, rather than
16 aboveground C stocks, are likely to be more useful for predicting tropical soil C stocks.
17 However, tropical forest root biomass is notoriously difficult to quantify, spatially variable, and
18 is not easily predictable as a proportion of aboveground biomass (14).

19 An alternative and widely-used approach for predicting soil C stocks at broad scales
20 relies on commonly measured abiotic properties, particularly climate and soil texture (1, 15).
21 For example, global-scale data show that soil C pools are generally greater in wetter forests (15).
22 A relationship between rainfall and soil C storage within tropical forests would be of particular
23 interest in the context of regional drying that is expected with climate change (16). Among soil

characteristics, clay content has been identified as particularly linked to soil C stocks, likely because of the importance of organo-mineral associations for soil C storage (17). An advantage of using abiotic properties like clay content to predict soil C is that data for soil texture are widely available, whereas root biomass data are relatively scarce (18).

An improved approach for predicting tropical soil C stocks may be to incorporate metrics that are strongly correlated to root biomass into the existing abiotic framework. In particular, soil phosphorus (P) and cations availability are commonly shown to limit plant growth in highly weathered tropical soils, which are leached of rock-derived nutrients and rich in nitrogen (N) (7, 8, 19). Root biomass in particular has been inversely related to soil P and/or base cation availability across a range of distinct tropical forests (20, 21). Similarly, root biomass and root growth in highly weathered tropical soils have shown consistent declines in response to elevated potassium (K) over fifteen years of factorial nutrient fertilizations in Panama (22, 23). These landscape-scale and experimental declines in root biomass in response to the availability of rock-derived nutrients likely indicate decreased plant C allocation to root biomass when nutrients are plentiful (24), which in turn reduces C inputs to soils. Root exudates are also increasingly recognized as an important contribution of root C to belowground stocks. Root exudates are produced as a plant strategy to promote the release of mineral nutrients via stimulated microbial decomposition and/or direct solubilization (25). Increases in rock-derived nutrient availability in tropical soils appear to suppress root exudates (26), similar to trends for root biomass, further decreasing root inputs to belowground C stocks. Thus, rock-derived nutrient concentrations might be a useful indicator of plant allocation to root activity in tropical forests, so incorporating base cations into predictive models could improve predictions of soil C stocks.

We studied 48 lowland tropical forest sites across the Isthmus of Panama to assess factors driving soil C stocks in tropical forests. The forests have a tropical monsoon climate and mean annual temperature of 26° C. The wetter Caribbean coast has a shorter dry season (~115 days), compared with the drier Pacific coast (~150 days). The sites cover extensive geological variation (Figure S1, Table S2) across a steep rainfall gradient (1756–3280 mm mean annual precipitation, MAP). Variation in soil nutrient availability across these sites corresponds primarily to shifts in geology, and soil properties are weakly or not at all correlated with rainfall (27), providing an opportunity to isolate the influence of rainfall from soil properties. We quantified total soil C, N, and P, resin-extractable P, extractable base cations, pH, soil texture and bulk density to 1 m depth in 1-ha plots at each site. Fine root biomass (<2 mm diameter) was sorted by hand. Soils were classified according to Soil Taxonomy (28), which provides an indication of soil weathering status. Aboveground biomass for all trees > 10 cm diameter at breast height was calculated using published allometry (29). Litterfall biomass was collected at a subset of 8 sites biweekly for one year (details in Methods and Materials).

We hypothesized that soil C stocks in tropical forests correspond to belowground dynamics, not aboveground plant growth. Specifically, we hypothesized that root biomass, soil P and cation availability, and rainfall predict soil C stocks across tropical forests.

Results

Overall, soil C to 1 m depth ranged from 7.3 – 20.3 kg C m⁻² across the sites, with an overall average of 13.3 ± 0.5 kg C m⁻². This average value for soil C stocks is between published averages to 1 m depths for similar forest types of 15.8 kg C m⁻² (ref. ⁴), and 11.5 kg C m⁻² (ref. (15)). The top 50 cm of soil contained an average of 75 ± 1% of soil C across sites, with a greater

1 concentration of C near the surface in less-weathered soil orders (Table 1). There was an even
2 greater concentration of root biomass in the top 50 cm of soil ($93 \pm 0.6\%$), with no variation
3 among soil orders (Table 1), suggesting that leaching of dissolved organic C from the soil
4 surface and rooting zone contributed to deeper soil C stocks.

5 In addition to the nearly three-fold change in soil C stock, the sites used here covered five
6 soil orders (Table 1), over 25 geological formations (Figure S1), a two-fold range in rainfall, a
7 20-fold range in base cations, and a >100-fold range in available P (Table S2). Thus, although
8 the data come from a relatively restricted geographic region, the diversity of environmental
9 conditions means that the results are likely to be broadly applicable over much larger
10 geographical ranges. The more strongly weathered soils were poorer in rock-derived nutrients,
11 more acidic, and contained greater fine root biomass and soil C stocks. However, most soil
12 characteristics were not clearly distinct among the orders (Table 1), indicating the importance of
13 using soil metrics like base cation availability rather than soil order in predictive efforts.

14 Across the 48 diverse tropical forest sites, aboveground biomass and litterfall were not
15 significant factors for predicting soil C stocks using a stepwise general linear model selection
16 process, which initially included all soil, aboveground, and climate data. Neither aboveground
17 biomass nor litterfall had a significant univariate correlation with soil C (Figures 1a & S3a).
18 Instead, soil clay content, root biomass, and precipitation were significant factors in the
19 minimum adequate general linear model for predicting soil C stocks to 1m (Table S4a). Soil clay
20 content (Figure 1b) and fine root biomass (Figure 1c) had the strongest univariate relationships
21 with soil C to 1 m, and also explained the majority of the variation in the minimum adequate
22 general linear model (Table S4a). Mean annual precipitation alone was only a weak positive
23 predictor of soil C ($R^2 = 0.10$, $n = 45$, $p < 0.05$, Figure S5), despite the nearly two fold difference

in rainfall across the sites. Predictors of soil C stocks to 0.5 m were similar, except that soil clay content was not a significant factor, and root biomass explained an even larger portion of the variation in the minimum adequate general linear model (Table S4b). Rainfall was a much stronger predictor of cumulative annual litterfall (Figure S3b), and especially of dry season litterfall (Figure S3c), showing significant negative relationships. Soil nutrients were not significant factors in the general linear model for predicting soil C stocks. However, a similar model selection process indicated that root biomass to 1 m was most strongly predicted by total extractable base cations, showing a logarithmic decline (Figure 1d).

Structural equation modeling was then used to infer mechanistic and directional relationships among all of the factors, and particularly to explore indirect linkages between soil nutrients and soil C stocks. Soil base cations, clay content, and rainfall as exogenous factors, with root biomass included as an endogenous factor linking base cations to soil C stocks, comprised the most parsimonious structural equation model for the data (Figure 2). Thus, the influence of base cations on soil C was mediated via effects on root biomass. This model explained nearly 50% of the variation in soil C stocks across the 48 sites.

Discussion

It was surprising that soil C was only weakly correlated with precipitation across these sites, despite a nearly two-fold change in rainfall over the gradient. This suggests that rainfall may not be an important factor driving differences in soil C stocks among tropical forests once soil fertility is accounted for, even when leaf litterfall is strongly responsive to rainfall. Similarly, five years of irrigation at a site near the middle of the Panama rainfall gradient did not result in changing root biomass or root turnover rates (30). However, a study in seasonal Amazonian

1 forests across soil fertility gradients showed decreased root biomass with declining soil moisture,
2 both within sites due to seasonality, and between sites due to experimental drying (31). These
3 contrasting results across observational and manipulative studies indicate that the potential
4 effects of climatic drying on root activity, and links to soil C storage, merit further mechanistic
5 research in tropical forests.

6 Base cations emerged here as a major driver of tropical forest root dynamics, with greater
7 investment in fine root biomass in cation-poor soils to maximize acquisition of these scarce
8 nutrients (24). This result highlights the benefit of including rock-derived nutrients as a driver of
9 plant and soil dynamics in tropical forest ecosystem models. Data on soil cations, as well as
10 texture, are available for many international sites (18), and can be estimated from geological
11 information and rainfall where data is unavailable (27, 32). Interestingly, no single rock-derived
12 nutrient was strongly correlated with root biomass or soil C across the sites. This contrasts with a
13 strong effect of K fertilization on plant growth and root dynamics been observed at sites near the
14 middle of this rainfall gradient (22, 23, 33). Also, it was surprising that P did not emerge as an
15 important driver of belowground dynamics across these sites, particularly since P varied so
16 strongly among these sites, and P has been shown to limit aboveground plant growth in other
17 tropical forests on highly weathered soils (8, 19). The general importance of base cations shown
18 here suggests that different rock-derived nutrients may be important among sites that vary in
19 geological substrate and soil type.

20 Overall, this work illustrates a decoupling between aboveground biomass and soil C
21 stocks in tropical forests, suggesting that roots, rather than aboveground plant growth or litter,
22 provide the primary source of C to tropical soils. Predicting how tropical soil C stocks will

respond to global change thus requires a mechanistic representation of links among soil cations and root dynamics in highly-weathered soils.

Materials and Methods

Study Sites

Soils were sampled from a series of 1 ha forest census plots located in the Panama Canal watershed, central Panama (Figure S1). Details of the plots and sampling of vegetation and soils have been reported previously (27, 34-36). Briefly all plots were in lowland tropical forests (elevation 10 – 410 meters above sea level) and included secondary, mature secondary, and old growth primary forests (34). The plots span a distinct rainfall gradient (annual rainfall ~1800 mm y^{-1} on the Pacific coast to ~4000 mm y^{-1} on the Caribbean coast) (34, 36). The mean annual temperature is 26°C and mean monthly temperature varies by < 1°C during the year (37).

The soils have developed on a range of geological substrates (Figure S1) (27, 34, 38, 39), including volcanic (basalt, andesite, agglomerate, rhyolitic tuff) and marine sedimentary (limestone, calcareous sandstone, siltstone, mudstone) lithologies. As a result, soils have marked variation in fertility (27, 35), which spans a range of taxonomic orders (27). Soils were classified by digging a profile pit adjacent to the southwest corner of each plot. Profiles were described by genetic horizon and samples of horizons were collected for chemical and physical analysis.

Soil Sampling and Analyses

Each 1 ha plot is marked on a 20 m x 20 m grid. Soil cores were taken to 100 cm in quadrats in the four corners and the center of each 1 ha plot (subsample $n=5$), in increments of 10 – 20 cm, 20 – 50 cm, and 50 – 100 cm. The 10 – 20 cm samples were taken with a constant

1 volume corer (5 cm diameter), and deeper samples taken with a 6.25 cm diameter auger. To
2 account for greater variation in soil roots and C at the surface, 8 additional soil samples from 0 –
3 10 cm depths were collected from alternate 20 x 20 m quadrats using the constant volume.
4 Stocks were calculated as the sum of the average values at each depth. This yielded 28 individual
5 samples per 1 ha plot, which were each analyzed for soil properties separately. In the two larger
6 plots (BCI – 50 ha, Fort Sherman crane site – 5.96 ha) additional surface samples were collected,
7 yielding a total of 50 samples on BCI (including samples to 100 cm in eight locations) and 44
8 samples at Fort Sherman (including samples to 100 cm in five locations), and a total of 8
9 locations were also sampled to 1m depth at BCI. Within-plot variation for root biomass and soil
10 chemistry is reported as the standard error of the 5 locations to 1m with plots (Table S2). The
11 within-plot relative standard error was 19% for root biomass to 1 m, and 13% for soil C stocks to
12 1m (Table S2). Including the addition surface soil samples for 0 – 10 cm depths decreased these
13 relative standard errors to 14% for surface roots, and 6 % for surface soil C stocks. These
14 additional measures were included in plot-scale averages for surface soils prior to summing by
15 depth.

16 Samples were all taken during the eight-month wet season, to avoid seasonal changes in
17 soil carbon concentrations (40), which could confound comparison among sites. The majority of
18 the plots were sampled during 2008 and 2009, with additional plots sampled between 2010 and
19 2014. Samples were returned to the laboratory within two hours of sampling and initially
20 screened (< 9 mm) to break up large aggregates, and stones and roots were removed by hand.
21 Soils were not sieved < 2 mm when fresh, because this is impractical for high clay soils. Fresh
22 soils were then extracted immediately using resin exchange beads for phosphorus, and within 24
23 h for exchangeable cations. Subsamples were air-dried for 10 days at ambient laboratory

temperature, sieved < 2 mm to isolate the fine earth fraction, and ground in a ball mill for total C and N determination. For soil profile pits, samples were air-dried and sieved as above.

For both plot and pit samples, total C and N were determined by combustion and gas chromatography using a Thermo Flash NC1112 Soil Analyzer (CE Elantech, Lakewood, NJ) and soil pH was determined in a 1:2 soil to deionized water ratio using a glass electrode. Total phosphorus was determined by ignition (550°C, 1 h) and extraction in 1 M H₂SO₄ (16 h, 1:50 soil to solution ratio), with phosphate detection by automated neutralization and molybdate colorimetry on a Lachat Quickchem 8500 (Hach Ltd, Loveland, CO, USA). Base cations were extracted in Mehlich-3 solution (41), with detection by inductively coupled plasma optical emission spectrometry (Optima 7300 DV, Perkin Elmer, Inc., Shelton, CT). Total exchangeable bases (TEB) was calculated as the sum of Ca, K, and Mg.

For profile pits, the concentrations of sand (0.053–2.0 mm), silt (0.002–0.053 mm), and clay (< 0.002 mm) sized particles were determined by the pipette method after pretreatment to remove salts (sodium acetate extraction), organic matter (H₂O₂ oxidation), and iron oxides (dithionite reduction) (42). In profile pits, bulk density was determined by the excavation method (43), removing ~1 L of soil and measuring the excavated volume of the plastic-lined hole with water. For the upper 20 cm of the soil, bulk density was calculated by weighing the total fresh soil mass from the constant volume core samples, and converting this to dry mass using oven dry weight (calculated by drying a subsample for 24 h at 105°C) and stone content of the samples.

Roots were exhaustively removed from each sample by hand (i.e. until no more visible roots remained), washed on a 250 micron sieve, oven-dried for 3 d at 60°C, and weighed. Root biomass was then calculated on an area basis using the core volume and depth for each sample, averaging depths across the plot and summing the depths to 50 cm and to 100 cm.

Total carbon stocks were calculated in kg/m^2 using bulk density and depth increments, averaging depths across the plot and summing the depths to 50 cm and to 100 cm. Bulk densities were for the fine earth fraction as a proportion of the total soil volume – i.e. accounting for the stone fraction (in both core samples and profile pits). Where samples were obtained to < 100 cm due to bedrock, the plot values were corrected based on the proportion of cores in the plot reaching a particular depth (i.e. average soil depth for the plot). However, plot averages were not corrected for floating boulders, where augering was prevented in some locations in the plot but soil continued below.

Litterfall

Fifty 1 m x 1 m litter traps were established within each of 8 1ha forest plots. This subset of the 48 plots represented both high and low fertility sites within a given rainfall range. Litter traps were distributed evenly across each plot, with a pair of traps in the center of each of the twenty-five 20 x 20 m quadrats. Litter from each trap was collected biweekly and dried at 65°C until mass stabilized (~ 48 hours), after which dry mass was measured.

Statistical Analysis

To identify significant predictors of soil C stocks we used preliminary backward stepwise linear regression analyses including all soil data for order, roots, nutrients, and texture, as well as aboveground biomass, and rainfall factors. We then included only potentially significant factors identified by these stepwise regressions in final linear models. Similar general linear model selection was used for predicting fine root biomass. We then ran post-hoc means separation Fisher's Least Significant Difference (LSD) tests to compare soil C, nutrients, texture, and root

biomass among soil orders. Where necessary, values were log transformed to meet assumptions of normality (e.g. total P and resin-extractable P).

We also analyzed the above relationships simultaneously using structural equation modeling (SEM) path analysis to assess mechanistic relationships among factors influencing soil C stock sizes. We used soil chemical and physical factors, aboveground biomass, and rainfall as exogenous factors, and soil C and root biomass as endogenous factors. We used SEM modification indices to add or remove specific pathways from the model. An initial model included soil P as an exogenous factor, but this was removed because of poor model similarity to the saturated model. The final default model (i.e. our model) was tested for overall similarity to the saturated model (i.e., ideal model) using common metrics of comparison (i.e., no significant difference from saturated model, Chi-square $p > 0.05$, GFI > 0.9 , NFI > 0.9 , RMSEA < 0.05). The model used 48 observations.

General linear models were performed using 13.0.0 JMP Pro software (SAS Institute Inc., 2016), and SEM path analysis was performed using SPSS AMOS 23 software (IBM, 2015). Statistical significance for all relationships and models was $p < 0.05$ unless otherwise noted, and means are reported \pm one standard error.

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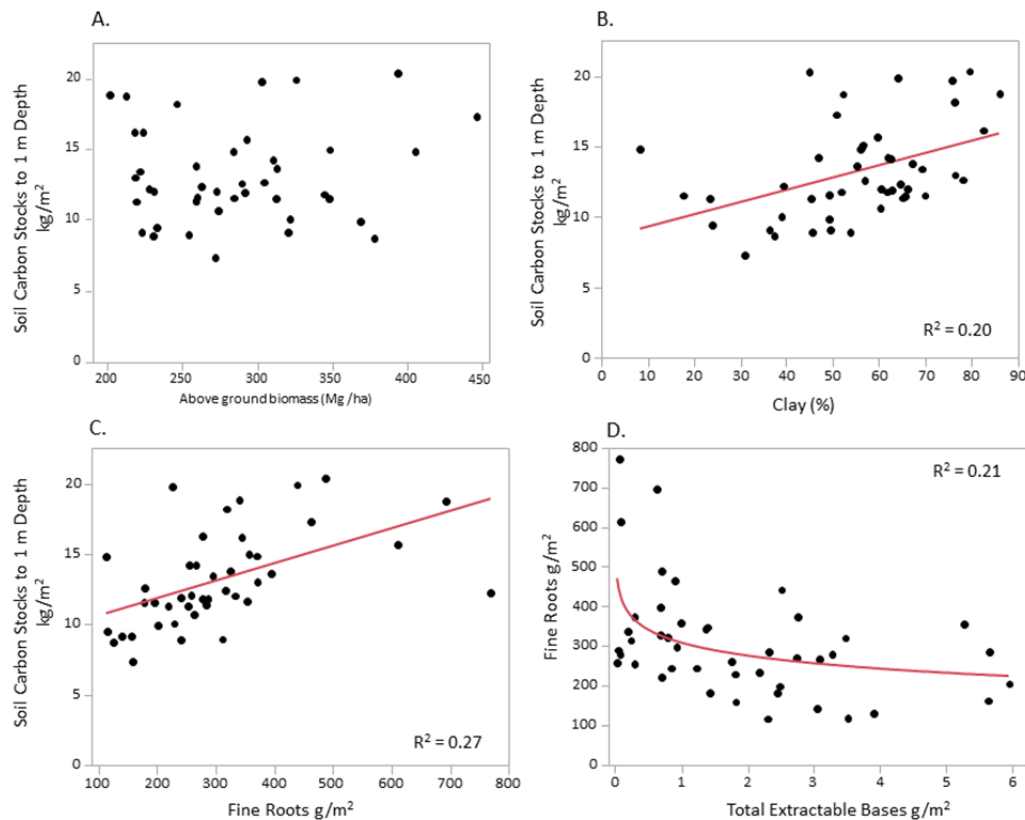
1 **Table 1. Soil chemical characteristics to 1m depth across tropical forest sites.** Soil C, nutrients, clay content, pH and fine root
2 biomass are shown for tropical forest sites across gradients in rainfall and geological substrate. In general, chemical characteristics
3 were only weakly ($R^2 < 0.05$) or not significantly correlated with rainfall across the precipitation gradient, other than total C and total
4 N ($R^2 = 0.10$ and 0.12 , respectively). Five soil orders were identified, including Inceptisols (Inc), Molisols (Mol), Alfisols (Alf),
5 Ultisols (Ult), and Oxisols (Ox). Inceptisols include modifiers because of the broad range of soil conditions found for this diverse
6 order. Modifiers include: aquic (Aq; periodic saturation at 40 – 75 cm depths), eutric (Eu; subsoil base saturation is high whether or
7 not the actual base concentrations are high or low), humic (Hu; high C), oxic (Ox; low effective cation exchange capacity). Means are
8 shown ± 1 standard error. Letters in columns show significant differences among soil orders using Fisher's LSD test ($p < 0.05$). Total
9 P and resin extractable P were log transformed for statistical tests to maintain assumptions of normality.

Soil Order (from least to most weathered)	# of sites (N)	Total C kg/m ²	% of C in the top 50 cm	Total N mg/m ²	Total P to 1 m g/m ²	Resin Extractable P g/m ²	Total Extractable Bases kg/m ²	Profile Clay (%)	pH	Fine Roots g/m ² ^	% of Fine Roots in the top 50 cm
Inc Aq	2	9.5 \pm 0.4 b	79 \pm 1 ab	813 \pm 35 b	199 \pm 67 ab	1.2 \pm 0.2 ab	4.5 \pm 1.5 a	49 \pm 0.1 ab	5.5 \pm 0.04 ab	172 \pm 31 c	92 \pm 0.5
Inc Eu	7	11.1 \pm 1.1 b	75 \pm 3 bc	1058 \pm 86 ab	349 \pm 90 ab	1.8 \pm 1.3 ab	2.5 \pm 0.6 b	51 \pm 7 b	5.5 \pm 0.3 ab	207 \pm 27 c	92 \pm 2
Inc Hu	4	14.8 \pm 1.9 ab	80 \pm 2 b	1471 \pm 274 a	263 \pm 48 ab	0.3 \pm 0.1 bc	1.7 \pm 0.5 bcd	65 \pm 4 ab	5.2 \pm 0.1 ab	294 \pm 30 bc	92 \pm 2
Inc Ox	3	13.8 \pm 1.2 ab	71 \pm 3 bc	1173 \pm 120 ab	184 \pm 40 ab	0.3 \pm 0.1 bc	0.6 \pm 0.3 cde	66 \pm 3 ab	4.7 \pm 0.3 bc	273 \pm 16 bc	96 \pm 2
Mol	3	10.8 \pm 1.7 b	90 \pm 6 a	865 \pm 88 b	248 \pm 25 ab	2.0 \pm 0.7 a	2.5 \pm 0.7 abc	47 \pm 12 b	5.6 \pm 1.1 ab	209 \pm 47 bc	93 \pm 5
Alf	13	13.5 \pm 0.9 ab	75 \pm 1 b	1250 \pm 82 ab	466 \pm 129 a	2.9 \pm 1.8 a	2.8 \pm 0.4 ab	51 \pm 5 b	5.9 \pm 0.1 a	294 \pm 30 bc	95 \pm 1

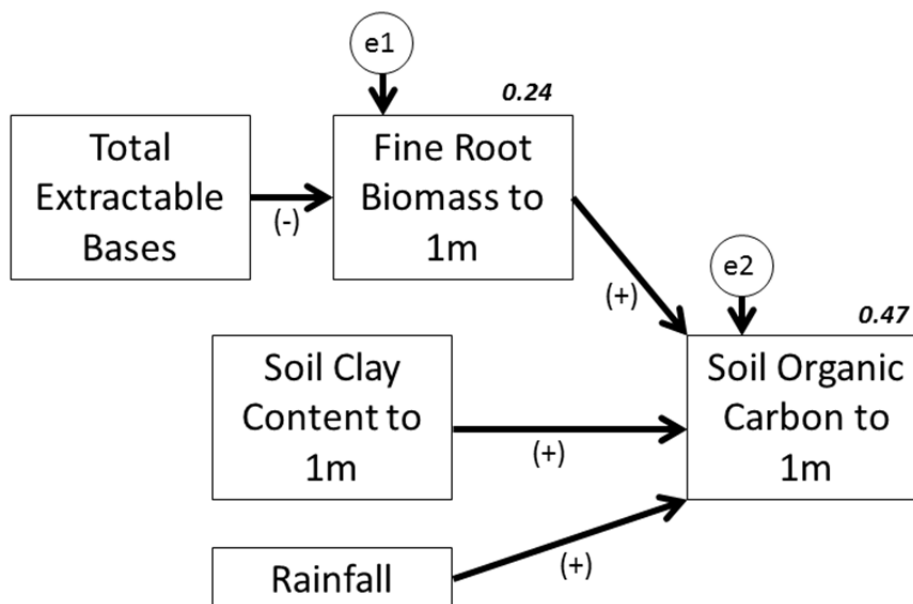
Ult	7	14.1 ± 1.0 ab	74 ± 4 bc	1026 ± 107 b	226 ± 56 b	0.3 ± 0.1 bc	0.2 ± 0.1 e	47 ± 5 b	4.4 ± 0.2 c	479 ± 97 a	94 ± 2
Ox	9	15.2 ± 1.4 a	69 ± 1 c	1381 ± 140 a	224 ± 52 b	0.2 ± 0.04 c	0.5 ± 0.1 de	67 ± 4 a	4.9 ± 0.2 bc	367 ± 23 ab	92 ± 1

1 ^ Root biomass was available for only 44 of the 48 sites.

1 **Figure 1.** Comparing predictors of soil C stocks, (A) above ground biomass showed no correlation ($R^2 = 0.009$, $n = 43$, $p = 0.52$),
2 whereas significant correlations were found for (B) soil clay content ($R^2 = 0.20$, $n = 47$, $p < 0.05$), and (C) fine root biomass ($R^2 =$
3 0.27 , $n = 44$, $p < 0.05$). (D) Fine roots, in turn, showed a logarithmic decline with extractable base cations ($R^2 = 0.21$, $n = 44$, $p <$
4 0.05). Aboveground biomass taken from (29). Equations for the significant predictors are: (B) Carbon Stock = $8 + 0.09 * \text{Clay}\%$; (C)
5 Carbon Stock = $9 + 0.01 * \text{Root Biomass}$; (D) Roots biomass = $307 - 47 * \log(\text{Total Extractable Bases})$.



1 **Figure 2. Structural Equation Model path analysis for the relationships between exogenous**
2 **factors (soil base cations, rainfall, and clay content), and endogenous factors (fine roots and**
3 **soil C stocks) is shown.** Bold values in italics above each endogenous factor show the squared
4 multiple correlation for that factor, giving the amount of variation in that factor accounted for by
5 all of its predictors (i.e., R^2). The sign below each arrow shows the direction of the relationship,
6 all of which are significant ($p < 0.05$). Correlations among exogenous factors were not significant
7 in this analysis. Factors in rectangles represent measured values, and circles represent
8 unmeasured error terms (e1 and e2) for each endogenous factor. Our model was not significantly
9 different ($p = 0.19$) from the “ideal saturated model” (chi-square 8.7, $df = 6$), indicating a good
10 fit for the data.



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